PHENOLOGY OF LINYPHIIDS IN AN OLD-GROWTH DECIDUOUS FOREST IN CENTRAL ALBERTA, CANADA

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ABSTRACT. Spiders in the family Linyphiidae are numerically dominant and show remarkably high diversity in northern forests, but relatively little is known about their phenology in northern latitudes of North America. We report a phenological summary of close to 6,000 individual linyphiids representing 17 species. These were collected by pitfall trapping during two snow-free seasons in an old-growth deciduous boreal forest in central Alberta, Canada. Three species of approximately the same body size, *Allomengea dentisetis* (Grübe 1861), *Bathyphantes pallidus* (Banks 1892), and *Lepthyphantes intricatus* (Emerton 1911), dominated the sample, and showed three distinct patterns of peak activity. This suggests temporal stratification as a possible mechanism that explains their co-existence. Four less commonly collected species within the same genus (*Walckenaeria*) showed similar seasonal segregation in periods of peak activity. Comparisons with other literature suggest the general phenology of many linyphiids is conserved across continental and global scales.

Keywords: Species co-existence, life-history, boreal forest, pitfall trapping

The family Linyphiidae (sensu lato) is the second most diverse spider family globally (Coddington & Levi 1991), and is notable in attaining greatest diversity in north temperate latitudes rather than towards the equator. As such, linyphiids dominate northern spider faunas (Helsdingen 1983). A notable biological feature associated with this high northern diversity is a flexibility of phenology (seasonal sequence of life history events) among members of the family. Linyphiid species display most of the phenological patterns known among spiders: multivoltine and univoltine strategies predominate in warmer climates, and the reproductive period of univoltines may occur in various seasons and for varying durations (Merrett 1969; Berry 1971; Draney 1997a, b; Draney & Crossley 1999). Northward, biennial and mixed annual-biennial strategies (in which some members of a population are annual and some are biennial) become more common (Schaefer 1977; Toft 1976, 1978). Different species overwinter as juveniles, adults, or (more rarely), eggs (Schaefer 1976, 1977), and some species actively feed and even reproduce during the northern winter (Huhta & Viramo 1979; Aitchison 1978, 1984).

Phenological flexibility has also been documented within linyphiid species, with longer cycles being displayed by more poleward populations (Almquist 1969; Toft 1976). Besides being a response to climate, phenological patterns are also associated with other ecological factors including vertical stratification of the spider (Toft 1978) and habitat type (Draney & Crossley 1999). Certainly, within any climatic regime, a variety of phenological patterns may be displayed by different linyphiid species.

Most of the work on linyphiid phenology has examined western and northern European populations experiencing relatively mild maritime-influenced climates (Juberthie 1954; Tretzel 1954; Almquist 1969; Merrett 1969; Toft 1976, 1978; De Keer & Maelfait 1987, 1988; Hauge 2000). With the exception of work in Finland (e.g., Huhta 1965, 1971; Palmgren 1972; Niemelä et al. 1994), less is known about linyphiid phenological responses to harsher continental boreal climates, such as

our study site in central Alberta, where seasonal variation is extreme. Some work has been done on the subnivean winter activity of spiders in these continental climates (Aitchison 1978, 1984). The present work examines growing season phenology of linyphiids in a sub-boreal climax deciduous forest. Our objectives include describing the phenological patterns of the common linyphiids as well as attempting to identify factors that might explain the variation in phenological patterns among the species in this system. We acknowledge that conclusions about phenology may be limited to our study location, sample period, and study years, but nonetheless hope to increase knowledge about a poorly understood component of the boreal spider fauna.

METHODS

Study site.—The study forest is located at the George Lake Field Station, located 75 km northwest of Edmonton, Alberta, Canada (53°57′N, 114°06′W). This old-growth deciduous forest has been left relatively undisturbed for over 100 years. The work described here was part of two larger projects investigating the relationship between ground-dwelling spiders and fallen logs, or downed woody material (Buddle 2001 a, b). The first project occupied an area of approximately 2.5 ha at the northeast section of the field station. The second project comprised about 3.5 ha in the northwest portion of the forest. Both projects were conducted in homogenous regions of this boreal mixed-wood forest, which is dominated by two *Populus* species: trembling aspen (*Populus tremuloides* Michx.) and balsam poplar (*Populus balsamifera* L.). Less common tree species in the area include birches (*Betula papyrifera* Marsh. and *B. neoalaskana* (Sarg.)), white spruce (*Picea glauca* (Moench)) and black spruce (*P. mariana* (Mill.) BSP). Further vegetation details can be found in Niemelä et al. (1992).

Sampling and spider identifications.—Ground-dwelling spiders were sampled with 88 pitfall traps in 1998 and 232 pitfall traps in 1999. All 88 traps in 1998, and 88 of the pitfall traps in 1999 were white circular (11 cm diameter) plastic containers sunk into the ground with the lip flush to the substrate surface (Spence & Niemelä 1994); 2–3 cm of preservative was used in the traps (silicate-free ethylene glycol) and a plywood roof mea-

suring 15 × 15 cm was elevated 2–3 cm above the traps to prevent flooding and trap disturbance. The additional 144 pitfall traps used in 1999 were smaller (6 cm diameter), made of clear plastic, and were covered with a circular plastic roof (11 cm diameter). Larger traps were placed 10–15 m apart; smaller pitfall traps were all 2 m from an adjacent trap (see Buddle (2001 a, b) for complete details regarding sampling design).

There has been some debate over the use of pitfall traps to sample ground-dwelling arthropods, as such traps are biased by the activity of the organism, and are influenced by such factors as trap material, type of preservative and color (e.g., Luff 1975; Adis 1979; Curtis 1980; Merrett & Snazell 1983; Topping 1993). However, pitfall traps have been shown to efficiently sample ground-dwelling spiders (e.g., Uetz & Unzicker 1976; Draney 1997 a, b; Buddle et al. 2000), and provided that no statements are made about absolute density, pitfall traps can be used to quantitatively assess periods of peak activities of male and female spiders (Toft 1976, 1978; De Keer & Maelfait 1987; Draney & Crossley 1999).

Sampling was continuous over the snow-free season in both years; in 1998 pitfall traps were placed in the forest on 4 May and removed on 10 September. Pitfall traps were opened from 20 April until 24 September in 1999. This provided 126 days of continual pitfall trapping in 1998 and 154 continuous trapping days in 1999. There were eight collection times (approximately every 15–20 days) in each year.

Samples were sorted and stored in 70% ethanol. All adult spiders were identified to species with nomenclature following Platnick (2003), and Buckle et al. (2001) for linyphiids. Voucher specimens of all taxa have been deposited in the Strickland Entomological Museum (Department of Biological Sciences, University of Alberta) and the Northern Forestry Centre Arthropod Collection, both in Edmonton, Alberta, Canada.

Data standardization and analysis.—Increasing sampling effort (i.e., number of traps) corresponds to an increase in the total catch of individuals (Niemelä et al. 1986). It was therefore necessary to standardize the collection data from 1998 and 1999 to account for variation in trapping effort. Without this standardization, it would be difficult to separate

true differences in relative abundance from simply differences in sampling effort. Prior to data standardization, however, species by sample accumulation curves were constructed using EstimateS Version 6.0 (Colwell 1997). This was to ensure that linyphiid species richness from 1998 (88 pitfall traps) and 1999 (232 traps) had leveled off, and thus represented complete samples. Only in this case would further standardization be justified. When this criterion was met, and when collections from different years were compared, pitfall trap data were adjusted to make catch data relative to a predetermined number of pitfall traps; since there were 88 traps in 1998 and 232 traps in 1999, data for both years were standardized to catches per 160 traps (average number of traps per year). Samples in 1998 were multiplied by 1.82 (i.e., 160/88), and samples in 1999 were multiplied by 0.69 (i.e., 160/232). Data were not standardized to account for differences in pitfall trap size (i.e., 6 cm versus 11 cm diameter) as Work et al. (2002) show catches of spiders do not vary significantly between these trap sizes.

Linyphiid species represented by fewer than 15 individuals in the collection were excluded prior to analyses as these would be too few to adequately assess phenological patterns. It was assumed that periods of peak male and female activity correspond to the peak reproductive period for the species (e.g., De Keer & Maelfait 1987; Draney 1997 a, b). Graphical analysis was used to assess this reproductive period and to evaluate the year-to-year variation in catches of the common ground-dwelling spiders. Results were compared to other published records and to information available on the same or closely related species from different geographic regions. Additionally, we measured the carapace width (CW) of our study spiders to ascertain overall spider size (Hagstrum 1971) to determine if any phenological patterns differed by species size. For these measures, a sub-set (i.e., 3–5 individuals) of both males and females were measured under a dissecting microscope fitted with an ocular micrometer. These measures were used purely in a relative sense, and thus sample sizes were small, and measures of variance were not used.

RESULTS

A total of 5,944 individuals representing 50 species of linyphiids were collected. Liny-phiids represented 32% of the total number of spiders collected experiment-wide, and 46% of the total number of species collected (see Buddle 2001a for complete species list). Of the linyphiids, 17 species were represented by $\geq$ 15 individuals, and these accounted for > 98% of the total number of linyphiids collected (Table 1). Three species accounted for most of the linyphiids (87.2% of the total linyphiids collected): *Allomengea dentisetis* (Grübe 1861), *Bathyphantes pallidus* (Banks 1892), and *Lepthyphantes intricatus* (Emerton 1911) (Table 1).

Species accumulation curves show that the observed species richness of the linyphiids had leveled off at about 80 samples in 1998 and about 65 samples in 1999 (Fig. 1). This illustrates that we adequately sampled linyphiids in this study, and comparisons across years are justified, as is standardization to account for sampling effort.

On a per-trap basis, about the same number of linyphiids were collected in 1998 (mean ($\pm$ SE) of 21.53 $\pm$ 1.39 spiders per trap, $n =$ 88)) as in 1999 (17.02 $\pm$ 0.57, $n = 232$). Standardized to 160 traps, we collected 3445.5 linyphiids in 1998 and 2722.8 in 1999. When the total male and female catch of the 17 linyphiid species is plotted by year and sampling time, it is apparent that males were more common in pitfall traps than were females. The peaks in female activity generally corresponded with the peak in male activity (Fig. 2). In both years female linyphiids were most commonly collected late in the season; males were more common in pitfall traps late in the season in 1998, but were less variable across collection dates in 1999 (Fig. 2).

Collections of the three common linyphiids showed three different phenological patterns, and these patterns were similar for both collection years (Fig. 3). *Allomengea dentisetis* was most active in August and September, *B. pallidus* in late July–August, *L. intricatus* in June. In general, females were less frequently collected than males, but their peak in activity corresponded closely to male activity (Fig. 3).

When the phenologies of all 17 linyphiid species are depicted, it is clear that periods of peak activity vary both in when males and females occur, and in the length of time both males and females are active (Fig. 4). For example, males and females of *L. intricatus*, *B. pallidus*, and *Microneta viaria* (Blackwall

Table 1.—Mean carapace width (CW, mm), number of females, and number of males, for 17 species of Linyphiidae collected by pitfall traps in 1998 and 1999, in a deciduous forest in north-central Alberta. Species arranged by size (descending).

| Species	CW	Females	Males	Total
Pityohyphantes costatus (Hentz 1850)	2.80	19	20	39
Allomengea dentisetis (Grübe 1861)	1.36	1068	1719	2787
Neriene clathrata (Sundevall 1830)	1.28	2	30	32
Helophora insignis (Blackwall 1841)	1.20	41	30	71
Lepthyphantes intricatus (Emerton 1911)	1.14	124	532	656
Oreonetides vaginatus (Thorell 1872)	1.13	13	60	73
Centromerus sylvaticus (Blackwall 1841)	1.02	1	14	15
Bathyphantes pallidus (Banks 1892)	0.88	433	1311	1744
Walckenaeria prominens Millidge 1983	0.82	3	64	67
Walckenaeria castanea (Emerton 1882)	0.81	26	0	26
Micronetta viaria (Blackwall 1841)	0.78	12	130	142
Lepthyphantes zebra (Emerton 1882)	0.78	2	30	32
Walckenaeria directa (O. P.-Cambridge 1874)	0.77	5	34	39
Sciastes truncatus (Emerton 1882)	0.66	0	36	36
Walckenaeria atrotibialis (O. P.-Cambridge 1878)	0.66	0	25	25
Pocadicnemis americana Millidge 1976	0.56	0	21	21
Diplocentria bidentata (Emerton 1882)	0.53	2	36	38
Total		1751	4092	5843
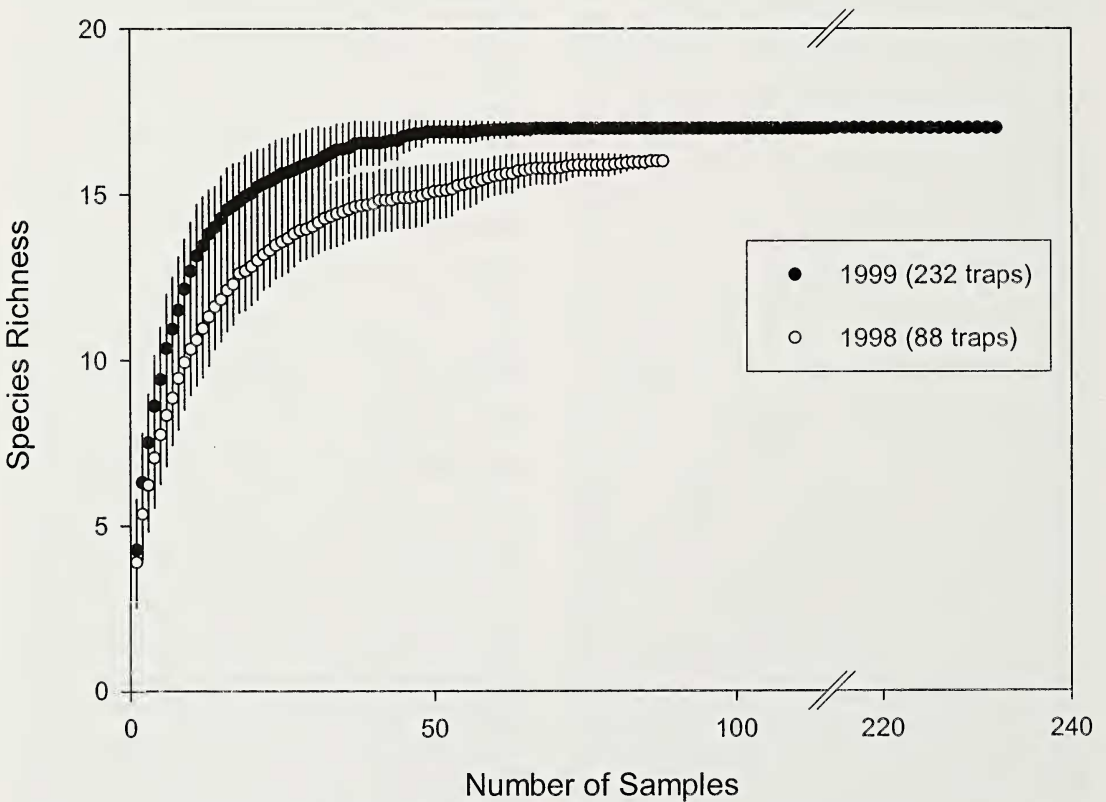
Figure 1.—Observed species accumulation curve of species richness by samples (pitfall traps) in 1998 (88 traps) and 1999 (232 traps). Data were re-sampled (randomly, without replacement) 50 times, error bars are ± 1 SD.
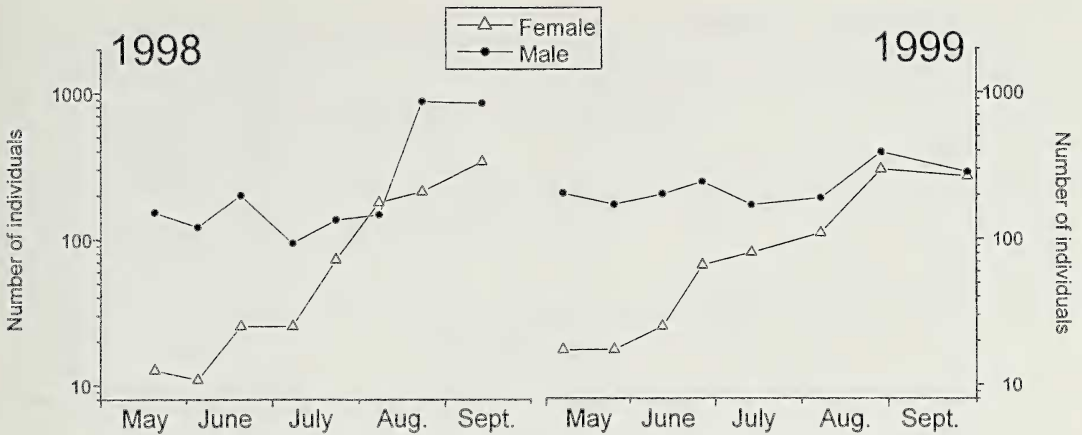
Figure 2.—Total number of male and female linyphiids (17 species) collected by pitfall traps in an old-growth deciduous forest. Note log-scale on axis. Number of individuals standardized to 160 pitfall traps.

1841) were caught in pitfall traps for much of the collection period, whereas many of the smallest linyphiid species collected show reduced periods of activity early in the season (e.g., *Diplocentria bidentata* (Emerton 1882), *Walckenaeria directa* (O.P.-Cambridge 1874) and *Lepthyphantes zebra* (Emerton 1882)) (Fig. 4). Smaller-bodied linyphiids were seldom collected past mid-summer whereas some of the larger-bodied species show higher catches in pitfall traps late in the season (e.g., *A. dentisetis*, *Helophora insignis* (Blackwall 1841) and *Centromerus sylvaticus* (Blackwall 1841)) (Fig. 4). Species within the same genus also show some differences in periods of peak activity. For example, collections of the four *Walckenaeria* species never overlap in time, and *L. zebra* occurs early in the season whereas *L. intricatus* shows a peak in activity about 3 weeks later (Fig. 4). It should be noted, however, that many of the species depicted in Fig. 4 were relatively rare in the collection (Table 1), so statements about their phenology should be interpreted with caution.

DISCUSSION

Linyphiids are dominant on the forest-floor in our old-growth study forest, in terms of both diversity and relative abundance; they represented almost half the total species collected and one third of the number of individuals collected. Our work represents one of the few detailed accounts of linyphiid phenology from northern regions of North America. We have presented data that shows three species, of approximately the same relative body size,

are remarkably common on the forest floor of north-central Alberta: *A. dentisetis*, *L. intricatus*, and *B. pallidus*. These species have also been shown to dominate the fauna of boreal-mixed wood forests throughout north-central Alberta (Buddle et al. 2000; Buddle 2001a). An important question is how these linyphiids might coexist on the forest floor, and the phenological summary may provide some clues.

It has long been suggested that seasonal segregation of similar-sized spiders might promote species co-existence (e.g., Breymeyer 1966; Williams 1962; Uetz 1977). In our work *A. dentisetis* shows a period of peak activity late in the season (August–September), *L. intricatus* early in the season (June), and *B. pallidus* in mid-summer. Thus, temporal segregation may be the mechanism that promotes co-existence of these linyphiids in northern boreal forests. We also see this general pattern within the genus *Walckenaeria* and *Lepthyphantes* from our collections. Future work will have to test this hypothesis, and it is difficult to claim generality from our limited collection time, and limited study area.

There are clearly other linyphiids that also co-occur with *A. dentisetis*, *B. pallidus*, and *L. intricatus*, but these may not directly interact with the three dominant species as they are either relatively rare in our collections, or are of a smaller body size (e.g., *Walkenaeria* species, *M. viaria*) (Table 1; Fig. 4), or they use herbaceous vegetation as additional foraging sites. For example, *H. insignis* is commonly collected by sweeping the vegetation in boreal
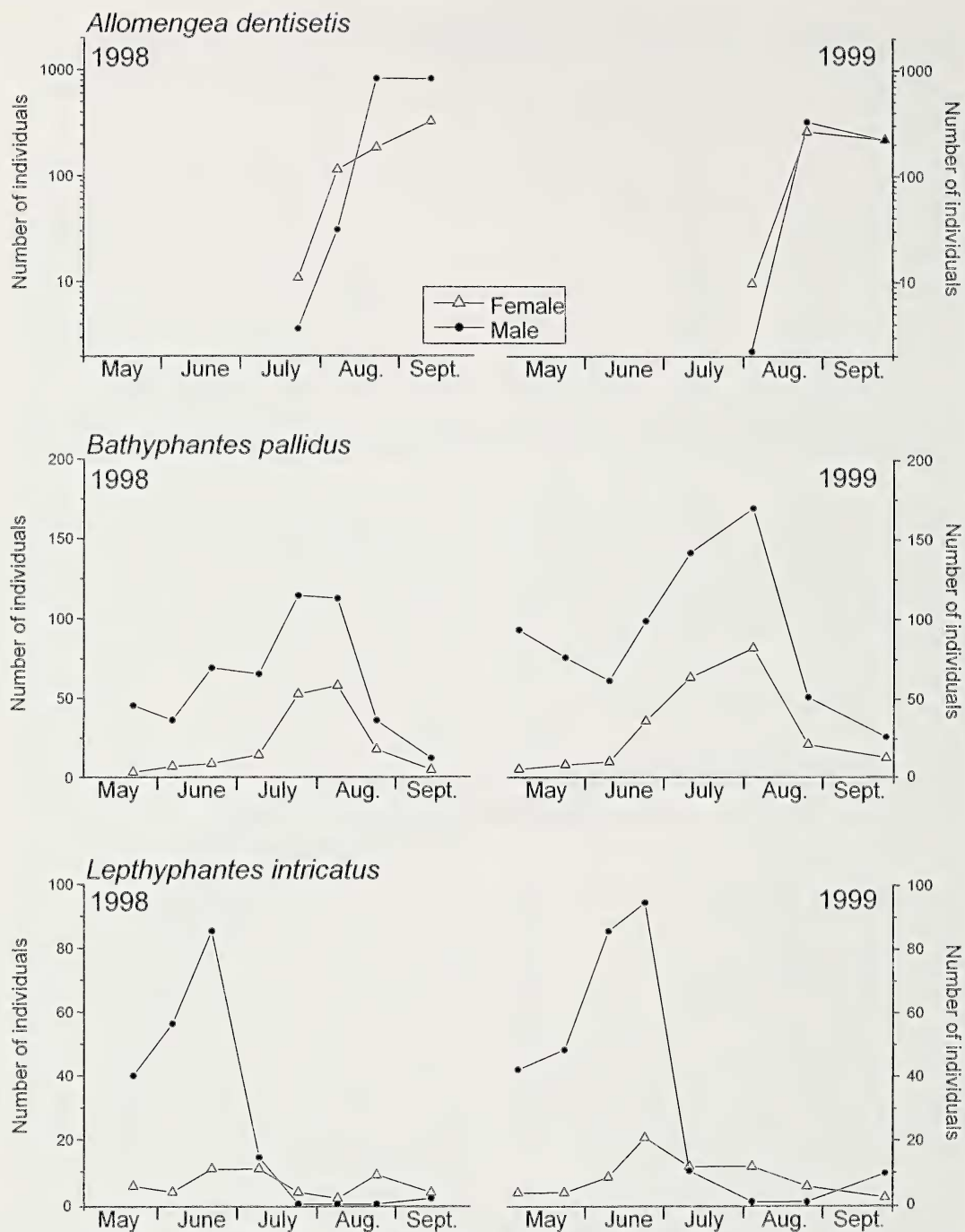
Figure 3.—Total number of male and female *Allomengea dentisetis* (top), *Bathyphantes pallidus* (middle), and *Lepthyphantes intricatus* (bottom) collected by pitfall traps in an old-growth deciduous forest. Note log-scale on axis of top graph. Number of individuals standardized to 160 pitfall traps.

mixed-wood forests (Buddle et al. 2000), and *H. insignis* and *Pityohyphantes costatus* (Hentz 1850) have often been observed in webs located in the herbaceous vegetation at our study forest (C.M. Buddle, pers. obs.). These species do use the forest floor as evident from our pitfall trap collections, but their main foraging location may be in the herba-
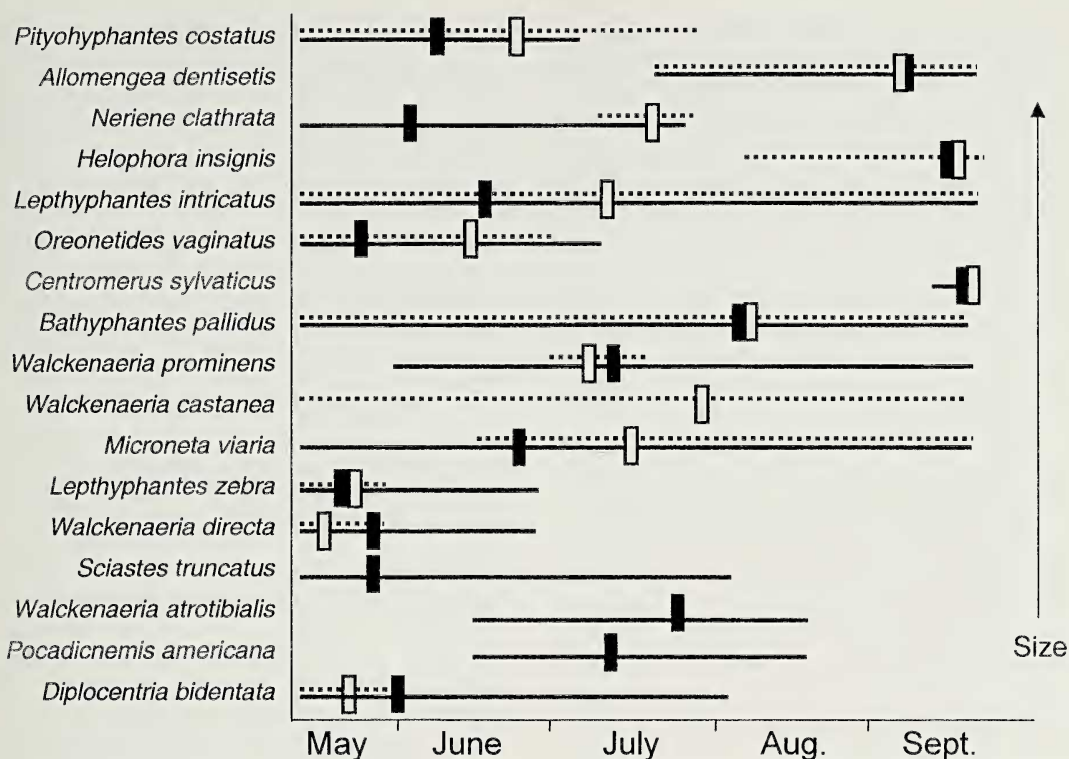
Figure 4.—Phenological summary of 17 linyphiid species collected over two years (pooled). Horizontal line indicates continuous periods when males (solid) and females (dashed) were collected. Vertical blocks represent peak activity of males (solid) and females (open), represented by weighted average of males or females collected by sampling period. Species size (smallest to largest, moving vertically) was determined by averaging carapace width for males and females.

ceous layer. Therefore, other larger-bodied species may interact with the three dominant species, but the frequency of interactions may be relatively low due to vertical habitat stratification (e.g., Turnbull 1960; Luczak 1966).

We can compare our phenological summaries with other published accounts of seasonal activity of linyphiids to determine whether any species or genera show consistent patterns across larger scales. We focus first on research by Niemelä et al. (1994) in Finland, as this work was also done in a mature forest in a climate with similar seasonal extremes as found in northern Alberta. Additionally, Niemelä et al. (1994) rely on pitfall trap data to ascertain peaks in spider activity, making comparisons with our study relevant, and several of the same species and genera are common to both studies.

Many of our results confirm research by Niemelä et al. (1994): *D. bidentata* occurs most commonly in early season, *M. viaria* is most frequently collected from June–early August, *Oreonetides vaginatus* (Thorell 1872) is most abundant early in the season, and *H. insignis* does not appear in collections until August. Therefore, the seasonal occurrence of some linyphiids is conserved, even on different continents.

Centromerus sylvaticus is known to be active in the winter under the snow layer in central Canada (Aitchison 1978). The entire genus is apparently winter active, with a cold season reproductive peak (Kronestedt 1968; Merrett 1969; Huhta & Viramo 1979; Draney 1997b). *Centromerus sylvaticus* has a low optimal temperature for postembryonic growth, which results in slow growth during the summer months, delaying maturity until late fall or winter (Schaefer 1977). In southern England, males and females peak in December and January, and females survive until July. Our data, showing high numbers of individuals in fall and none in the spring, may indi-

cate that in harsh winter climates, reproduction occurs before winter, and adults do not generally survive to the next spring.

The four species of *Walckenaeria* in our data set all displayed a stenochronous pattern of adult activity, with short peaks occurring in late winter (Fig. 4, *W. directa*), June–July (*W. prominens*), Mid–July (*W. atrotibialis*), and early August (*W. castanea*). Examined species within the large genus *Walckenaeria* all seem to be univoltine (Tretzel 1954; Merrett 1969; Huhta & Viramo 1979; Draney 1997a); whether this trait is constant within the taxon remains to be seen.

Several authors (Schmoller 1970; Muma 1973; Doane & Dondale 1979) have suggested that the male pitfall catch peak is the best indicator of the mating period of a species, since males are trapped as a result of their mate-searching behavior. Female catch is related to either foraging behavior in order to obtain food for egg production, or behavior related to oviposition activity. In many species (such as our *P. costatus*, *L. intricatus*, and *M. viaria*, Fig. 4) the male peak occurs well before the female peak, although in other species (*A. dentisetis*, *H. insignis*, *C. sylvaticus*, *B. pallidus*, *L. zebra*, Fig. 4) the peaks are essentially simultaneous. In no species is the female peak well before the male peak; cases with earlier female peaks occur only in species with few trapped individuals, and the pattern could be a result of sampling error (e.g., *W. directa*, $n = 39$ and *D. bidentata*, $n = 38$, Table 1). Additionally, we found that more males than females were collected in our pitfall traps. This is also largely attributable to the differential locomotory activity associated with reproduction; males tend to wander extensively in search of mates. In two cases we collected more females of a species than males (Table 1). This may be due in part to oviposition behavior. For example, Toft (1978) suggested that many species, including *H. insignis*, lay their eggs in the leaf litter, even if they forage higher in the vegetation. Koponen (1987) also reported highly female-biased pitfall catches of two linyphiid species, *Hybauchenidium gibbosum* (Sørensen 1898) (95% female, $n = 127$) and *Zornella cultrigera* (L. Koch 1879) (100% female, $n = 36$).

Linyphiid spiders are important predators in northern forests, given their ubiquity, abundance, and high diversity. Phenological data can be useful to predict times during which species are likely to occur and also allow us to better predict potential biological interactions and population responses to human-caused and natural ecosystem alterations, depending on the timing of these events. Phenological data is useful but is not known with precision for most linyphiid species. Useful phenological insights can be garnered from ecological data collected for other purposes, and we hope future work will further test patterns uncovered in our study forest.

ACKNOWLEDGMENTS

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